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THE RHEOTROPISM OF ROOTS.

FREDERICK C. NEWCOMBE.

(WITH FIFTEEN FIGURES)

(*Concluded from p. 283.*)

VI. LOCATION OF THE SENSITIVE AREA.

SEVERAL experiments were made by Juel[11] to locate the sensitive area. His tests were of two kinds. He cut off the apical 1.5^{mm} of the root of *Vicia sativa*, exposed the seedlings thus prepared to the water current, and found that rheotropic curves followed somewhat more promptly and with greater angles than in uninjured roots. So many seedlings were employed, and the responses were so uniform, that we are probably justified in accepting the results as demonstrating a rheotropic sensitiveness of the roots in the absence of the apex. Juel's other device consisted in covering the apical portion of roots with caps of collodion. These caps varied from 2 to 7 or 8^{mm} in length. Sufficient experiments were made with the shorter caps to show that the root was sensitive throughout its elongating zone. With the caps 7 to 8^{mm} long only six roots were tested, and of these only two gave reliable positive curves, two remaining straight, and two growing through the collodion and bending positively. Juel explains the curves with collodion caps as due either to the pressure of the water being felt through the collodion or to the penetration of the water stream through the collodion.

1. *Experiments with water-jets.*

My first series of experiments to determine the extent of the sensitive area was made by the employment of fine jets of water directed against various small areas of the root. Each seedling used was fixed by wet cotton in a perforation in a cork closing the lower end of a short glass cylinder 1.5 to 3^{cm} in height. The seedling thus projected both above and below the cork. Its upper part was packed in wet cotton, while 5 to 10^{mm} of its root projected for the application of the water-jet. At frequent intervals water was put into the small cylinder, and this slowly percolated through the cotton and ran down over the root, thus insuring constant moisture. The water-jets were secured by bringing the water from an elevated reservoir through glass and rubber tubes to small glass nozzles passed through corks which were adjustable in height on small movable standards. The water-jets as they left the nozzles were from 0.2 to 0.5^{mm} in diameter. Each jet was adjustable by a screw-clamp applied to the conducting rubber tube.

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[11] Untersuchungen über den Rheotropismus der Wurzeln. Jahrb. Wiss. Bot. 34:507.

This method would seem to offer a somewhat delicate means of locating the sensory area of the root. The majority of roots gave a positive response, but most of the roots did not grow very well. This behavior may be ascribed to various factors. In spite of the precautions taken, the exposed roots of the seedlings were not always everywhere kept covered with moisture; the nutations of the roots made it extremely difficult to keep the water-jet on a precise area, though the experiments were constantly watched and readjustments made; and it was practically impossible always to keep the water stream from circling around the root, thus greatly extending the root surface exposed to the water stream. Besides these objections, it may be well to note that a fine water-jet properly meeting the root affects only a very small surface, and it may be that a larger area must be stimulated to bring forth a ready response. The following table will present the main features of results obtained when the water-jets were applied to the apical millimeter of the root-tips.

TABLE VIII.

GIVING RESULTS OF WATER-JETS APPLIED TO THE APICAL MILLIMETER OF THE ROOT.

Species	Period	Number of roots	+ Curves	− Curves	Neutral
Helianthus annuus ...	7 hours	4	4	..	..
Brassica alba........	4 to 6 hrs	14	6	2	6
Totals............	....	18	10	2	6

That the relatively small number of positive responses in the foregoing tests with *Brassica alba* does not necessarily indicate a lack of sensitiveness in the root-tip is shown by results following the application of the water-jet to the elongating zone, this part having been proved sensitive by Juel's work as well as my own. In one experiment with the highly sensitive *Brassica alba*, the water-jet met the root 2 to 5^{mm} above the tip, yet after a period of twelve hours, of the six roots only two were positive, while one was negative and three were neutral. However, in a total of four experiments of this nature with *Brassica alba*, the seventeen roots showed twelve positive, two negative, and three neutral. This is certainly less equivocal than the results obtained from the same species when the water-jet was applied to the apex.

In conclusion it may be said that the experiments with the water-jets have indicated a rheotropic sensitiveness for the apical millimeter of the root.

2. *Experiments with cylinders of paper and of collodion.*

Another series of experiments to locate the sensitive area was tried with cylinders of paper and others of collodion, in which were cut apertures to admit the streaming water. *Fig. 14* shows the form of these devices. The paper cylinders were made of thin paper held in form by paraffin, and the bottom closed by a bead of paraffin. The collodion cylinders were cast over small rods of sugar, the sugar being subsequently dissolved out by immersion in water. To prepare these rods commercial cane sugar was dissolved by heat and rolled into small rods between the hands. These were then rolled to the desired diameter between plates of glass. Apertures were cut at any desired location in these cylinders, a vane was attached to the upper end to keep the cylinder in a constant position, and enough paraffin applied to make the whole slightly buoyant in water.

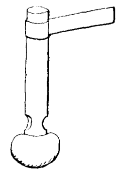

FIG. 14.—Illustrating the construction of collodion and paper cylinders used in locating the sensitive area.

These cylinders or stockings were slipped over immersed roots as the seedlings were suspended over basins of water like those already described. When the basin was set in revolution, the stockings behaved well, but results were not forthcoming. The failure was probably due in part to the interference of the cylinders with the direction of the water stream, and in part to their mechanical interference with the curving of the roots.

3. *Experiments with glass tubes.*

The third and most satisfactory method for determining the extent of the sensitive area was the employment of glass tubes of several patterns, by means of which definite parts of the roots were exposed to the water streams in the revolving glass basins, and definite parts were shielded from the streams. The experiments are divided into two groups, those testing the sensitiveness of the apical millimeter or millimeter and a half, and those testing the rest of the root.

a. Testing the sensitiveness of the apex of roots.

To determine the sensitiveness of the apex of roots, straight glass tubes 3 to 4^{cm} in length and 3^{mm} internal diameter were used. Seedlings of suitable size, usually not more than a half centimeter longer than the tubes, were selected for experiment. The tubes were held in water and the seedlings passed in, after which a little wet cotton was pressed in around the seedling by the use of a needle whose point was broken off. The cotton was pressed in firmly enough to hold the seedling in position, yet not too firmly, to allow the seedling to be moved up or down the tube. Preparations thus made were fastened to bars of wood by means of strips of blotting paper and rubber bands, as shown in *fig. 15*. The bar of wood, with its load, was next suspended with the glass tubes dipping into water in a glass basin on a centrifuge, the seedlings were carefully adjusted so that their tips projected 0.5 to 1^{mm} from the glass tubes, and the revolving apparatus was set in motion. In recording the results given below, data as to temperature and velocity will be omitted.

Each could be given, but it will be sufficient to say that temperature was in each case from 21 to 26° in water, and the velocity of water current was from 150 to 500^{cm} per minute.

With *Zea mays* (popcorn) three experiments were made. In the first, eleven roots were used. The tips were never allowed to project from the glass tubes more than 2^{mm}. Every half hour, or oftener if necessary, the roots were pulled up a little to bring them back to 1^{mm} of exposure. After 4 hours, four roots had bent positively with angles ranging from 5 to 20°; the other seven roots were neutral. The second experiment was, in conditions, in every way like the first, except that the period of the test was 8 hours. Ten roots were used, and five of them curved positively with angles of 15 to 20°; the other five roots remained neutral. The five curved roots at the conclusion of the experiment had all bent over in contact with the edges of the glass tubes. The third experiment was quite like the others, except that the roots were not allowed to protrude more than 1.5^{mm} from the tubes, and the period was 7 hours. Ten roots were used, and at the end of the trial six had bent positively and the other four were neutral. One of the responding roots gave an angle of 5°, one of 15°, and four of 20°.

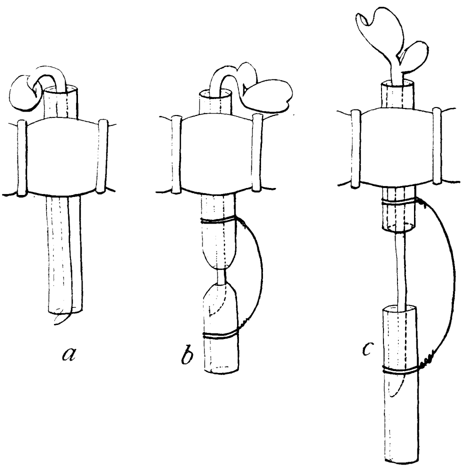

FIG. 15.—Illustrating the use of glass tubes in locating the sensitive area of *Raphanus sativus: a*, form of tube used in experimenting with the apex of the root; *b*, form used for exposing a narrow zone; *c*, form used in shielding a long apical section and exposing a long section back of the shielded portion.

With *Raphanus sativus* (Early Long Scarlet), results are still more decisive. In the first group thirteen seedlings were used. In 2¾ hours after the revolution began five roots were positive, in 5 hours ten were positive, and in 6 hours all thirteen were positive. These roots had never more than 2^{mm} exposed. Another set of twenty seedlings with 1 to 1.5^{mm} of the apex exposed gave, after 8 hours, nineteen roots decidedly positive and one neutral. In a third experiment, the roots had a maximum of 1^{mm} exposed, each root being raised to 0.5^{mm} of exposed tip as soon as it approached the millimeter limit. Nine seedlings were used, and in 9 hours five roots had become positive, while the other four remained neutral. A final experiment, conducted exactly like the last, gave, after 9 hours, six roots positive with angles of 10 to 20°, while the other four roots remained neutral.

Unless serious objection can be brought against these experiments, they prove that the apex of the root is sensitive to the rheotropic stimulus. It may be objected by some that too much of the root was exposed, so that the elongating zone was affected by the current. This stricture can hardly hold when we consider that in one experiment with *Zea mays* not more than 1.5^{mm} was exposed, and in two experiments with *Raphanus sativus* not more than 1^{mm} was exposed. The root cap of this Raphanus has an axial depth of 0.3 to 0.4^{mm}, so that not more than 0.7^{mm} back of the cap was exposed, and this amount only for a small fraction of the period of the experiment. It may be thought that possibly there was a current in the tube itself at a greater or less distance above its lower end. This objection has been answered, to some degree at least, by two devices. In one experiment the lower ends of the tubes were contracted so that the root nearly filled the aperture; in the other experiment the space between root and tube was lightly filled with cotton. In both cases good curves were formed. In the first experiment, the bend in the roots took place above the constricted mouth of the tube, while the tip of the root extended obliquely through the narrowed opening. In the second experiment the bend took place in and below the cotton, the cotton not offering a very great resistance. Another answer to the foregoing objection lies in the fact that roots that were kept retracted within the tubes so that their tips were level with the lower end of the tube never gave any curves. Contact with the side of the glass tube never effected any curvature. Scores of roots have been allowed to grow down through glass tubes, and many have by filling with cotton been pressed against the tubes as the roots grew out through the lower end, yet none have curved in quiet water. If we consider the proportion of the number curving to the total number of roots under experiment, we shall see that there is no ground here for objection to the assumption of the sensitiveness of the root-tip. In *Zea mays* almost half responded positively, and these were almost as many as have, in other experiments with the whole root uncovered, responded in the same time. In *Raphanus sativus* forty-three in fifty-two responded positively. That these curves were responses to the stream of water is readily believed when it is seen that there was not a single case of a negative curve. The curves were all relatively small, because the tubes stopped the progress of the curving; the curves were nevertheless decisive, being usually 15 to 20°, and to the author, who has during the past five years seen thousands of irritable curves in roots, there can be no doubt of the result.

From the foregoing experiments it may safely be concluded that the apex of the root is sensitive to a rheotropic stimulus.

b. Testing the sensitiveness of the root back of its apex.

In order to determine what part of the elongating zone of the root is sensitive, paired glass tubes constructed as shown in *fig. 15*, *b*, *c* were used. The tubes were 3^{mm} in internal diameter, were held together with fine annealed steel wire, and in each paired tube the ends that faced one another were narrowed. The tubes with their contained seedlings were held on supports as in the preceding group of experiments, and adjustments for the desired exposure of the root-surface were made as then, by moving the seedling up or down in the tube. It might be thought that the movement of seedlings up and down the tubes would interfere with results, either by injury to the roots or by bringing a different flank to meet the current. To overcome this objection the seedlings were in several experiments fastened to the supporting bar by themselves and the encasing tubes were fastened to the same bar by a separate band just below the band holding the seedlings. Such a preparation enabled the glass tube to be moved up or down while the seedlings remained fixed. Results showed that there was no advantage in this more troublesome preparation, and it was discarded as unnecessary.

All of the following experiments were made with *Raphanus sativus* (Early Long Scarlet), the roots of this plant being insensitive to diffused light, and light being necessary at frequent periods of observation.

For the first series of experiments the apical 2^{mm} of the root were kept below the opening between the two parts of the paired tube, and not more than 2^{mm} of root were exposed to the water current. In one set of seven seedlings, at the end of 7 hours' revolution, five roots were positive 5 to 40°, while the other two roots were straight. In a second set of six roots, at the end of 4 hours 40 minutes, five were strongly positive, and the sixth root was straight.

These results show that the part of the root just above the apical 2^{mm} is sensitive.

In the next series of experiments ten seedlings were used whose apex was covered for a distance varying from 3 to 8^{mm}. Above the covered portion of the root, a portion 5 to 8^{mm} long was exposed. After 8 hours eight roots were positively bent and two roots were straight.

Five experiments, including forty-eight seedlings, were made, in which 10^{mm} of the apex of the roots were covered, and the root left exposed for 5 to 8^{mm} above the covered part. The duration of the experiments varied from 10 to 11 hours. At the end, thirty-four roots were positive, three were negative, and eleven were neutral.

Two experiments, including a total of twenty-three seedlings, were made in which 15^{mm} of the apex were covered, and 5 to 8^{mm} above the covered part were exposed. The duration of the experiments was in one case 10 hours, in the other 12¾ hours. Of the twenty-three roots, ten became positive, two negative, and eleven remained neutral.

Two experiments, including nineteen seedlings, were made, in which 20^{mm} of the apex of the roots were covered, and the roots left exposed for 5 to 8^{mm} above this portion. One experiment ran for 9 hours, the other for 11 hours. Of the nineteen roots, seven became slightly positive, four slightly negative, and eight remained straight.

The results here recorded are most interesting. They teach that the root is sensitive to the rheotropic stimulus at a considerable distance back of the elongating zone. The elongating zone in this variety of *Raphanus sativus* extends but 5^{mm} back of the tip. This fact I determined by marking ten roots with India ink, and observing them with a horizontal microscope at intervals during 24 hours. The roots were kept immersed in water. Growth was observed to take place in some roots in the first 4^{mm} only, and in the others in the first 5^{mm}. No root showed any elongation of the sixth millimeter. All conditions for growth were favorable, and good growth took place in each root.

Objectionable conditions were in these experiments removed as far as possible. The experiments were all performed within a period of five weeks, the temperature was held within a variation of one degree, the revolution of the basins was the same speed for all, giving in each experiment a range of velocities from 150 to 500^{cm} per minute, and the duration of the last three series, which are the only ones whose results might *a priori* be called in question, was nearly alike. To lessen the chances, if there were any, of a feeble stream being set up within the tubes themselves, the lower end of the lower tube was in some cases closed with a plug of cotton, in other cases closed by fusing. In still other experiments not only was the lower end of the lower tube closed, but cotton was packed around the root at its entrance into the lower tube. Thus it would seem that all possibility of a current within the tubes was excluded. The closing of the ends of the tubes is, however, not advisable; for it tends to produce distortion in the roots after 12 to 15 hours of 23° or over. This may come from the lack of oxygen or the accumulation of the excreta of the root. The experiments recorded above, therefore, were performed with open tubes, except for the narrowing at the inner ends, as shown in *fig.* 15. The tips of the roots in all the experiments were kept from 5 to 15^{mm} removed from the lower open ends of the tubes. In several tests where the whole root was enclosed in a tube, the tip coming even with the lower open end, there was no curvature. The possibility, therefore, of curvature being caused by streams within the tubes may be dismissed.

The experiments show a decreasing sensitiveness in the roots from the region of the elongating zone back to a position at least 15^{mm} from the apex. When 20^{mm} of the apex of the root were covered there seemed to be some disturbance of the root but no pronounced directive influence. There were in this case proportionately more than twice as many negative curves as in any other set, while the number of positive curves was much less than in other experiments.

It is worth noting that the percentages of positive curvature in the four different sets show a constant decrease, being 80 per cent. in roots with 3 to 8^{mm} covered, 71 per cent. in roots with 10^{mm} covered, 44 per cent. in roots with 15^{mm} covered, and 32 per cent. in roots with 20^{mm} covered. The angles attained in these curvatures were often as great as the tubes would allow, and averaged 17° in the first series, 19° in the second, 18° in the third, and 11° in the fourth. Thus it is shown that when 20^{mm} of the root were covered the positive responses were relatively so few and gave such small angles that one may well suppose that the limit of sensitiveness has been approximated. Not so, however, with the portion of the radish root 15^{mm} from the tip; of the twenty-three seedlings used, nearly half gave good positive curves, and there were only two negative curves. The small number of negative curves is excellent evidence for the reliability of the result; for the absence of negative curves shows that the positive curves cannot be charged to pathological distortion.

If this evidence is reliable, it shows that the rheotropic stimulus is received and transmitted by a part of the root 10^{mm} removed from the limit of the elongating zone, and 12^{mm} from the part which first curves. Remarkable as this result may seem, I believe it will stand the test of time. One must master a certain amount of technique to obtain success; but the technique once learned, the preparation is easy and the results sure.

C. RESULTS WITH OLDER PLANTS.

I. WITH SECONDARY ROOTS.

It cannot be inferred *a priori* that the secondary roots of non-sensitive primary ones would be found non-sensitive, nor can it be inferred that the secondary roots of sensitive primary ones would be found sensitive. It seems to be true, however, that secondary roots are sensitive or insensitive according to the sensitiveness or insensitiveness of the primary root. Berg[12] found both primary and secondary roots positively rheotropic in *Zea mays*, *Fagopyrum tataricum*, *Tropaeolum majus*, *Lupinus albus*, *L. luteus*, *Vicia faba*, *V. sativa*, and *Helianthus annuus*, while neither order of roots in *Soja hispida* was sensitive. My own results are as follows:

Seven seedlings of *Cucurbita pepo* with short lateral roots protruding were suspended with roots immersed in a basin of water for two days. During this time, the basin was revolved for two periods, once for 24 hours and once for 16 hours. The lateral roots that could be counted as long enough for experiment numbered from thirty-five to forty, the shortest being 1^{cm} and the longest 5^{cm} The temperature was 24 to 26°, and the velocity of current ranged from 300^{cm} for the slowest to 1200^{cm} per minute for the most rapid flow. All roots, both primary and secondary, grew well and grew straight.

Tropaeolum majus was tested in the same way, but in velocities ranging from 150 to 600^{cm} per minute. Only ten secondary roots were present, and unfortunately the test lasted only 12 hours. All roots grew straight.

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[12] Studien über Rheotropismus. Lunds Universitets Årsskrift. **35**^{2}: no. 6.

Zea mays (a yellow dent variety) was abundantly employed in several experiments. The seedlings with primary and secondary roots present were suspended in the usual way along the diameter of several glass basins. The temperature varied from 21 to 24° in air, and the velocity ranged from 150 to 600^{cm} per minute. The duration of each test was one week. Some hundreds of secondary and many tertiary roots were present in the latter half of the week. The primary roots, as usual in this species and variety, contorted very badly; the secondary and tertiary roots grew without contortion, and nearly all became strongly positively curved. Only two or three took a negative course, and not more than seven remained neutral.

The secondary roots of *Fagopyrum esculentum* were tested on ten seedlings which had their roots immersed in the water of a revolving basin for 41½ hours. The temperature varied from 23 to 28°, and the rate of flow ranged from 125 to 600^{cm} per minute. There were fifty secondary roots 1^{cm} long or over. Of the secondary roots, fifteen became positive, four negative, and thirty-one did not curve. Of the main roots, seven became positive, one became contorted, and two remained straight.

From the foregoing results one can hardly generalize, because the experiments are too few. Yet it is evident that in the two plants, *Cucurbita pepo* and *Tropaeolum majus*, whose main roots had been found insensitive, or but weakly responsive, to a rheotropic stimulus, the secondary roots are insensitive also; and that in the *Fagopyrum esculentum*, the secondary as well as the primary roots are sensitive, but the former much less sensitive than the latter. For the variety of *Zea mays* used, it may be said that the main roots always contort so badly in water that their relations in rheotropism cannot be determined. Other varieties of *Zea mays* (popcorn and those employed by Jönssen, Berg, and Juel) we know to be positively rheotropic in the main root. The experiments here recorded show the secondary and tertiary roots to be rheotropic also.

II. WITH ROOTS OF MATURING PLANTS.

To obtain the roots of older plants for experiment, special preparation was necessary. Flower pots were chosen of medium size, the bottom broken out and wire netting placed for a bottom. The netting had meshes a little over 2^{mm} in diameter. In these crocks seeds were planted, and the crocks set on a stone slab outdoors, the season being summer. This treatment prevented any great growth of roots through the bottom of the crocks. When the plants had grown to suitable size, the crocks were set into battery jars, the crocks closing the opening of the jars and leaving a free space as a damp chamber below the crocks. The whole preparation was then sunken into the ground, and thus the light was excluded. Such preparations soon gave a good growth of roots down below the crocks. When the roots had attained suitable size, the crocks were lifted out of the jars and set over glass basins with the exposed roots immersed in water. By the revolution of the glass basins, a current of water was generated as in the preceding experiments. The roots that were used in the experiments were probably in no case primary. It is most probable that all primary roots had died at the tip in growing through the bottom of the crock while the crock was sitting on the stone slab.

Hordeum vulgare was used when the plants were 30 to 37^{cm} above ground and were flowering. Twenty-six good roots appeared. The first curves were noted in 20 hours after the revolution of the water basin began. The experiment continued for 50 hours, in air temperature of 24°, and velocities ranging from 100 to 400^{cm} per minute. Twenty-two roots bent positively with angles of 45 to 90°, and four roots remained neutral.

Cucurbita pepo, in the same conditions of temperature and current as Hordeum, was kept in the water stream for 84 hours. The plants were a month old and were in flower. Fifty roots were subjected to the current, but not one bent from a straight course.

Helianthus annuus, a month old, was tested in the same manner as the foregoing plants. There were thirty-two good roots. Of these, twenty became positive, five negative, while seven did not curve.

Fagopyrum esculentum, the plants having nearly ripe fruit, and treated as the foregoing species, gave twenty-four roots for experiment. After 38 hours, fourteen roots were positive, four were negative, and six were contorted.

Raphanus sativus, a month old, furnished twenty-eight roots for experiment. No curves appeared for the first 20 hours. After 50 hours of revolution of the basins, twenty-one roots had positive curves of 45 to 90°, three were contorted, and four were straight.

Again it appears here that the sensitiveness of roots to a stream of water is neither lost nor gained in increasing age of the plant. In the preceding chapter it was indicated that the secondary roots are less sensitive than the primary. The same conclusion is much more strongly indicated by the experiments just narrated. Yet one may not argue too strongly from these last experiments. Plants growing in crocks are probably not very vigorous, and tests have shown over and over again that lack of vigor inhibits irritable responses. To cite a single case, I may say that a crock of plants of *Helianthus annuus*, not in a vigorous condition, was kept for 60 hours over revolving water with two dozen roots immersed, and no curvatures appeared.

D. NATURE OF THE RHEOTROPIC STIMULUS.

The nature of the rheotropic stimulus has not been determined. In the paper read before the American Association for the Advancement of Science[13] in 1896, I suggested that the rheotropic stimulus was pressure. Juel (*l. c.*) has renewed the suggestion, but no one has offered any direct evidence. The physiological importance of rheotropism is difficult to perceive, and hence one suspects here a case where the mechanism developed in response to some biologically important stimulus is set in motion by some other stimulus, as an electric current throws a muscle into contraction.

[13] BOT. GAZ. **22**: 242. 1896.

If one considers the more common responses of roots, he will soon become convinced that rheotropism is none of these. Since the publication of Czapek's [14] hypothesis as to the means of the perception of the geotropic stimulus, one may even think of the possible connection of rheotropism with geotropism. If the direction of gravitation is perceived by the radial pressure of the layers of cells upon those more deeply lying, the pressure on one side of the root in flowing water would stimulate the gravitation pressure, and might call forth a pseudo-geotropic curve, the rheotropic curve. Since, however, it is almost certain that the gravitation stimulus is perceived by only the apical 1 to 2^{mm} of the root, and the rheotropic stimulus is perceived by 10 to 20^{mm} of the root, it is not probable that rheotropism is simulated geotropism.

Rheotropism is not necessarily connected with heliotropism; for several species, *e. g.*, *Raphanus sativus*, have been found rheotropic which are not heliotropic. Nor is rheotropism connected with hydrotropism; for, as demonstrated by Pfeffer,[15] in hydrotropism only the apical 1 to 2^{mm} of the root is sensitive. Rheotropism cannot be traumatropism; for in the former the response is the same when the stimulus is perceived by the tip of the root as by the part farther back. Aerotropism has been appealed to by many to account for various curvatures of roots in water. I have tested several species of plants with rheotropic roots for aerotropism, by bringing submerged chambers of air within a few millimeters of the side of root-tips which were several centimeters below the surface of water. The confined air was in most cases separated from the roots by parchment paper. In other cases there was no membrane intervening, the submerged chamber being tilted so as to hold the air, while the roots were brought within a few millimeters of the edge of the air-containing chamber. In none of these cases were the roots caused to deviate more than 5 to 10° from the vertical direction, and the majority of roots in any one preparation were unaffected. Rheotropism, therefore, is not aerotropism.

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[14] Untersuchungen über Geotropismus. Jahrb. Wiss. Bot. **32**: 224.

[15] On this topic see Rothert, Flora **79**: 212. 1894; and Czapek, Jahrb. Wiss. Bot. **35**: 316.

Lastly, we may ask what the probability is that rheotropism is response to pressure. On the one hand we know that the water current exerts one-sided pressure on the roots, and we are at a loss to perceive any other influence which the current may exert. On the other hand, a response of roots to pressure, either a positive or a negative response, has never been demonstrated. Sachs[16] thought he had found roots positively thigmotropic when stimulated on the elongating zone; but the curves produced were traumatic, as a forthcoming paper of mine will show. Darwin's[17] supposed negative thigmotropic curves of the root tip have been shown to be traumatropic by Wiesner[18] and Spalding.[19]

If the rheotropic curving is due to pressure, it might be thought that solid particles in the water stream might cause either an earlier or a greater response. Two experiments were tried with seedlings of *Helianthus annuus*, in one of which wheat flour was stirred into the water stream and in the other clay was used. In each case a control was set up with roots in water filtered through a Berkefeld filter. While the water was revolved the solid material was stirred up every half hour. In the first test the roots gave a readier response in the filtered water than in that containing the flour; in the second case, responses appeared at about the same time and the roots attained about the same angles in both basins.

There is no evidence to show that roots are sensitive to pressure, and until that is shown it is idle to speculate as to the relation of rheotropism and thigmotropism.

E. SUMMARY.

I. STATEMENT OF CHIEF RESULTS.

The foregoing pages narrate the results obtained in experiment with thirty-two species of plants. These thirty-two species include all plants but two that have been tested by others for rheotropism, and twenty-one species that have never been experimented with before. In my own work and that of others, therefore, thirty-four species have been used. Of these, twenty have proved positively rheotropic, and fourteen have been found insensitive. *Rheotropism cannot therefore be said to be a general phenomenon.*

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[16] Arbeit. aus. d. bot. Inst. Würz. **1**: 437.

[17] Power of movement in plants, 1880, p. 129.

[18] Das Begwegungsvermögen der Pflanzen, 1881, p. 139.

[19] On the traumatropism of roots. Annals of Botany **8** : 423. 1894.

The foregoing experiments teach nothing more clearly than that sensitive species differ greatly in the degree of sensitiveness to a stimulating water current. As with almost any other irritable response, one may arrange species in a series according to their rheotropism. The twelve species of plants reported as rheotropic by Jönsson, Berg, and Juel should all be accounted as but feebly or moderately sensitive as compared with five *Cruciferae* and *Zea mays* (*everta* Sturt.) as reported in this paper.

The fourteen species found insensitive are distributed through nine families, and the twenty sensitive species through six families. Several species in a single family have been tested in the case of the *Gramineae* with five species in five genera, the *Leguminosae* with ten species in seven genera, the *Cruciferae* with six species in three genera, and the *Cucurbitaceae* with two species in two genera. All five species of the *Gramineae* are sensitive, five species of the *Leguminosae* are sensitive and five insensitive, five species of the *Cruciferae* are sensitive and one insensitive, and both species of the *Cucurbitaceae* are insensitive. Two or more species in each of five genera have been under experiment, and in each genus the species have been either all sensitive or all insensitive. *There is an indication therefore that the roots of genetically related plants behave alike toward a water current.*

On the other hand, of two varieties of *Lupinus albus* tested, one gave no response, while the other showed itself fairly responsive; and of the varieties of *Zea mays*, all the large fruited forms were but feebly affected, while the popcorn was very sensitive.

The four aquatic plants and the semi-aquatic *Nasturtium officinale* are none of them sensitive to the water stream. It is hardly probable, therefore, that rheotropism stands in any biological relation to water plants.

Berg in his paper was unable to determine whether the velocity of water current had any effect on the response. Juel, working only with *Vicia sativa*, obtained only straight or negatively bent roots in velocities as high as 1800^{cm} per minute, while positive curves appeared in the majority of cases in velocities from 1.8 to 1800^{cm} per minute. The highest percentage and the strongest curves were found in velocities between the extremes named; the lower limiting velocity was not found. In my experiments data were obtained on the action of several species in varying velocities of water. *It has been shown that velocities above* 1000^{cm} *per minute give generally negative (mechanical) curves, that the optimum velocity lies between* 100^{cm} *and* 500^{cm} *per minute, and that velocities below* 50^{cm} *per minute bring fewer and slower responses with smaller angles.* The remarkable result was obtained of finding the main root of *Raphanus sativus* rheotropic in a velocity less than 1^{cm} per second, while the directive influence of a velocity of 2^{cm} per second was no longer obeyed by the main roots of *Brassica alba.* It should be remembered, however, that the character of the curve in these very weak currents differs greatly from that shown in optimum currents, the actual curves in the latter becoming mere positive inclinations in the former.

The latent period for rheotropism was stated by Berg to be for *Zea mays* one hour with the reading microscope; while that of *Vicia sativa* according to Juel is two hours. Table VII on p. 272 of this paper shows the shortest latent period obtained for eight species of plants. There it is seen that species differs greatly in time of response, though the latent period for all is relatively long compared with that for geotropism. Compared with the heliotropic response, the geotropic response of *Brassica alba* and *Helianthus annuus* is not much slower. The actual latent period for rheotropism has not, however, been determined by anybody for any plant. In the first place, the experiments have not been carried on in the optimum temperature for growth; and in the second place, all experiments, so far, have been interfered with by geotropism. In my own study some experiments were made in which the effect of gravitation was sought to be eliminated by using the centrifuge revolving with vertical disk under water. The plan is wholly feasible, but in my work was not pursued far enough to give final results.

In the competition between geotropism and rheotropism, which comes into play from the method of experimentation, some roots attain only a small deviation from the vertical, some reach 45°, and some 90°, the last seeming to overcome their geotropism wholly. When the definitive angle is attained by a root, this angle is retained for an undetermined period. Only in the case of weak stimuli have roots been observed to lose their responsiveness to the water stream and to resume their vertical position while the water stream still continued.

The occurrence of the geotropic counter-curve is explained in assuming that the resultant position of equilibrium for roots in which geotropism and rheotropism are competing is different in the apical 2^{mm} from what it is in the part of the root farther back. This difference in position of equilibrium for the two parts of the root is due to the extent of both the sensitive and the motor zones. The first curve in ordinary geotropic bending being located, in roots of medium size, not more than 2^{mm} from the apex of the root, the apex bends down when rheotropism is carrying the root beyond the resultant position of equilibrium. The geotropic sensitiveness being confined to the apical 2^{mm}, the part farther back is, by the sinking of the sensory zone, released to some degree from its impulse to bend downward. As there is in the experiment a continuous rising of the part of the root posterior to the apical 2^{mm} as growth goes on, we must assume that the motor zones for geotropism and for rheotropism, in this kind of experiment, are in different parts of the root—the former being within 2^{mm} of the apex, and the latter three or more millimeters from the apex.

The present paper has given evidence for the rheotropic sensitiveness of at least 15^{mm} of the apex of the root. By means of fine jets of water directed against the apical millimeter of the roots of *Helianthus annuus* and of *Brassica alba*, ten positive curves in a total of eighteen roots were obtained. The other eight roots all remained straight. The relatively small proportion of curves was doubtless due to the shortness of the period of the experiments and to the technical difficulties involved in the method. By shielding from the water stream by a glass tube the whole root of *Zea mays* (popcorn) except the apical 1.5 to 2^{mm}, fifteen positive curves and sixteen straight roots resulted. Unfortunately the periods of the experiments for this plant were only from 4 to 8 hours. Had they all extended to 12 hours there would doubtless have been a much larger proportion of curves. The absence of any negative curves, however, shows that the curves obtained were really rheotropic. The apical 0.5 to 1.5^{mm} of the root of *Raphanus sativus* exposed to the water stream by the same method as used with *Zea mays* (popcorn) gave thirty positive curves and nine straight roots in a total of thirty-nine seedlings. In two of these experiments there was never more than 1^{mm} of root tip exposed to the current, yet even in this case more than half the roots became positive. *It may be claimed, therefore, that the rheotropic sensitiveness of the very apex of the root has been demonstrated.*

That the root of *Vicia sativa* is rheotropically sensitive throughout its elongating zone was indicated, but not demonstrated by the experiments of Juel (*l. c.*). He employed too few seedlings, especially in the case in which 7 to 8^{mm} of the apex of the root were covered with collodion caps, where he used only six roots and obtained only two reliable curves. In my experiments forty-eight seedlings of *Raphanus sativus* had their apical 10^{mm} covered with glass tubes, and thirty-four gave positive response in a water stream. In another series with the same species, twenty-three roots had their apical 15^{mm} of the root covered, and ten gave positive curves. When, however, nineteen seedlings of Raphanus had 20^{mm} of the apex of their roots covered, only seven very weak positive curves appeared, while there were four weak negative curves, and eight straight roots. *It may be said, therefore, that the roots of Raphanus sativus are rheotropically sensitive for more than 15^{mm} of their apex*, but scarcely, if at all, sensitive beyond 20^{mm} of their apex. In preceding pages it has been shown that *the rheotropic sensitiveness decreases proximally from the limit of the elongating zone*. Since the elongating zone in *Raphanus sativus* has been shown to extend less than 6^{mm} from the apex of the root, *we have in this plant, and probably in other rheotropic plants also, a sensory area ten or more millimeters distant from the limit of the elongating zone, and therefore a transmission of stimulus through a distance of twelve or more millimeters from tissue that has ceased to elongate.*

Rheotropism is not confined to the primary root. Berg (*l. c.*) states that he observed it in the secondary roots of eight species of plants, while it was absent in one species. My tests extended to four species. Putting Berg's results and mine together, eleven species with both primary and secondary roots have been tested for the rheotropism of secondary roots. Of these eleven species, eight have shown themselves positive in both primary and secondary roots, two have shown themselves neutral in both orders of roots, and one (*Tropaeolum majus*) was found sensitive in both orders by Berg, but feebly sensitive in the primary and neutral in the secondary roots by me. Berg makes no statement as to relative sensitiveness of primary and secondary roots. In my experiments the secondary roots of *Fagopyrum esculentum* were less sensitive than the primary, but the secondary and tertiary roots of *Zea mays* (yellow dent) were more sensitive than the primary. *One may conclude at least that the secondary roots are sensitive or insensitive according to the sensitiveness or insensitiveness of the primary root.*

All the experiments of former investigators of rheotropism have been carried on with seedlings. In my study the roots of older plants have been tested in five species. The seedlings of four of these species had proved themselves rheotropic, and the roots of the same species a month old were found rheotropic also. In the case of the fifth species neither the roots of the seedlings nor of the older plants were sensitive. *As far as the study has extended, therefore, it has been found that rheotropism is neither gained nor lost in the development of a plant from seedling to near maturity.*

As to the nature of the rheotropic stimulus, there is no direct evidence. I still incline to the notion of pressure, as expressed in my paper before the American Association for the Advancement of Science in 1896. As yet, however, no one has demonstrated in the roots of plants any kind of a response to pressure.

II. TABULATION OF SPECIES EMPLOYED AND THEIR RHEOTROPIC BEHAVIOR.

Family	Species	Rheotropic behavior
Gramineae	Zea mays L. Yellow dent	Feebly sensitive
	" " Sweet	Feebly sensitive
	" " Popcorn	Highly sensitive
	Triticum vulgare Vill	Feebly sensitive
	Hordeum vulgare L	Highly sensitive
	Secale cereale L	Highly sensitive
	Avena sativa L	Highly sensitive
Hydrocharitaceae	Elodea canadensis Michx	Insensitive
Naiadaceae	Potamogeton perfoliatus L	Insensitive
Liliaceae	Allium cepa L. Bulb	Insensitive
	" " Seedlings	Insensitive
Ranunculaceae	Ranunculus aquatilis L	Insensitive
Cupuliferae	Quercus alba L	Insensitive
Cucurbitaceae	Cucurbita pepo L	Insensitive
	Citrullus vulgaris Schrad	Insensitive
Cruciferae	Brassica alba Boiss	Highly sensitive
	Brassica nigra Koch	Highly sensitive
	Brassica campestris L	Highly sensitive
	Brassica oleracea L	Highly sensitive
	Raphanus sativus L	Highly sensitive
	Nasturtium officinale R. Br	Insensitive
Geraniaceae	Tropaeolum majus L	Feebly sensitive
Polygonaceae	Fagopyrum esculentum Moench	Highly sensitive
Euphorbiaceae	Ricinus communis L	Insensitive
Leguminosae	Vicia faba L	Feebly sensitive
	Vicia sativa L	Fairly sensitive
	Lupinus albus L	Fairly sensitive
	Phaseolus vulgaris L	Insensitive
	Phaseolus lunatus L	Insensitive
	Phaseolus multiflorus Willd	Insensitive
	Pisum sativum L	Fairly sensitive
	Glycine hispida Maxim	Insensitive
	Dolichos lablab L	Insensitive
	Lathyrus odoratus L	Fairly sensitive
Compositae	Helianthus annuus L	Fairly sensitive

In addition to ten of the species in the foregoing table, Berg tested *Lupinus luteus* L. and *Fagopyrum tataricum* Gaertn., both of which he found sensitive.

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